THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SEVENTH SERIES.]

No. 40. APRIL 1901.

XL.—*On the Mutual Relations of the Arctic and the Antarctic Faunas* *. A Lecture by Professor Dr. Georg Pfeffer, Custos of the Museum in Hamburg.

In response to repeated invitations, I have undertaken to deliver this lecture on the relations of the faunas of the higher northern and southern latitudes; and in doing so it is my intention to submit to you not detailed observations but general reflections. I shall therefore bring the subject before you in a setting of general historical geography, but at the same time I shall touch upon all the theories which have been published, without, however, mentioning by name the various authors or giving the text of their conclusions. I have to ask you to take my lecture for what it is intended—an orienting introduction for those who have a practical or general interest in a study which is at present attracting so much attention—the investigation of the highest latitudes of our earth.

Descriptive.

According to temperature, the surface of the ocean may be divided into three natural regions: first, the tropical region, with a high temperature which varies but little throughout

* Translated by Margaret R. Thomson from "Ueber die gegenseitigen Beziehungen der arktischen und antarktischen Fauna," Verh. deutsch. zool. Ges. ix. (1899) pp. 266–287.

the year; second, the polar region, with low temperature and slight variations; thirdly, the temperate region, with moderate temperature and great yearly variations. To these natural thermal zones there correspond similar faunistic regions; but this statement requires certain qualifications, chiefly in regard to what we are here especially considering—the animal life of the ocean-floor, the Benthos of Haeckel.

The arctic fauna shows zonal development, or, as it has been called, circumpolarity, very perfectly; while in the antarctic fauna, with the weak development and the wide separation of the coast-area characteristic of that region, circumpolarity is much less observable.

The tropical fauna is relatively uniform in its representation throughout the whole tropical zone, yet, conditioned by the formation of continents on the one hand, and by the unique horizontal and vertical motion of the water on the western tropical coasts on the other, faunas of a peculiar kind are differentiated on the west coasts of Africa and America.

In the fauna of the temperate zones circumpolarity diminishes considerably, giving place to the development of local faunas. This corresponds to the enormous formation of continents in the north, and the wide separation of coast-regions in the south; and the local occurrence of extraordinary yearly variations of temperature has a similar influence. The parts of the temperate zone which border on the tropics show likeness in many respects to the tropical zones, and those bordering on the polar zones similarly approach these, and we speak therefore of two subtropical faunas, and of a boreal and a notal fauna.

Besides the horizontal decrease in warmth there is a corresponding vertical decrease, inasmuch as—speaking quite generally—the temperature of the ocean, from the surface to the floor, gradually falls, so that all gradations from tropical warm to polar cold water are to be found.

Two regions may be distinguished in the water of the open sea: first, a superficial region, through which light penetrates, and in which both variations of temperature and the movements of the water are felt; and, secondly, a deeper region, reaching to the ocean-floor, constant in temperature and without either light or water-movements. For pelagic animals this division at once suggests a corresponding faunistic division; but, with regard to the dwellers on the ocean-floor, other considerations have to be taken into account; and accordingly the ocean, and the fauna which it

contains, may be divided vertically into the three following regions :—

First: the surface-water,—the warmest of all the vertical zones, with variations in warmth, with movement of the water, with the influence of light, and therefore with plant-growth, with a terrigenous floor consisting of rock, gravel, and sand. This region reaches, according to the locality, from the surface to a depth of from 50–150 fathoms. The expressions "surface-water" and "surface-fauna" are here used as practically equivalent to "littoral zone" and "littoral fauna."

Second: the subsurface-water,—cool, without variations in warmth, without light, without plant-growth; its floor lies on the slope of the continents and is covered with terrigenous mud. According to locality, this region reaches to a depth of 600–1000 fathoms; its fauna consists only of the mud-eaters, and is therefore economically dependent on supplies from other regions, particularly on the assimilating flora and fauna of the adjoining surface-water. The fauna of this region resembles the fauna of the surface-water of higher latitudes.

Third: the deep water, the deep sea,—resembling the subsurface zone in its lack of variations of warmth, of light, of plant-growth, and water-movement; its floor is the bottom of the ocean, and is covered with fine slimy ooze or clay of pelagic origin; its fauna is economically independent of that of the coasts, because of the great distance between them, but, on the other hand, it is dependent on the pelagic animals, whose dead bodies form its food-supply. Apart from archaic or highly specialized forms, the fauna of this region has an arctic character; that is, it resembles the surface-fauna of the highest latitudes.

Disregarding for the present the nature of the ocean-floor, and considering the water with reference to its temperature alone, we have, first, a tropical warm water occurring only as the surface-water of the tropical zone; second, a cool subsurface-water, which, in the higher temperate zones, gradually passes over into the surface-water of a similar temperature; third, a cold, deep water, which covers the whole ocean-floor, and within the polar zones passes over into equally cold surface-water. Thus the cold water has a universal spatial distribution over the whole earth, the cool water an almost universal distribution over the torrid and temperate zones, while the warm water occurs solely as the surface-water of the tropics.

Corresponding to this there is, first, a warm-water fauna, which is developed only in the surface-water of the tropics;

second, a cool-water fauna, which extends over the whole subsurface-water of the tropics and temperate zone, as well as over the surface-water of the latter; third, a cold-water fauna, spreading over the whole floor of the ocean, and embracing also the surface- and subsurface-water of the polar regions.

The subsurface fauna is certainly not identical with the surface fauna of higher latitudes, nor the deep-water fauna with that of the polar regions; but there is, in the first place, a marked "habit resemblance" between them; and, in the second place, there is really a gradual transition, in the higher and highest latitudes, between the vertically distributed and the horizontally distributed faunas; and, thirdly, a number of northern and southern species do succeed in spreading far in the direction of the equator through the subsurface-water, just as many species of polar animals are found on the ocean-floor at a great distance from their surface-region. The historical aspect of this point will be dealt with farther on.

Herewith we conclude the first and descriptive portion of our study.

Problem of Historical Development.

The fundamental idea of present-day science, that whatever exists is intelligible only in the light of its history, its evolution, leads us at once to the second part of our subject —the problem, namely, of the historical development of the present conditions of our ocean-fauna.

The fauna of the present day may be described as the impoverished fauna of the Tertiary period. Though a few genera of the present day reach considerably farther back, yet faunistic pictures from before the Tertiary period wear so unfamiliar an aspect that, for the study before us, which is intended only to interpret present conditions, it seems unwise to follow the roots of our fauna farther back than the Early Tertiary or the Later Cretaceous period.

Tropical Conditions in North Temperate Latitudes.

In the Early Tertiary period there was in our regions a fauna of tropical character reaching at least to the latitude of Copenhagen, and we must therefore assume that, at that period, these latitudes enjoyed a climate of tropical warmth.

The legitimacy of this inference has been doubted by some palæontologists: firstly, because it might be assumed that genera, which now occur only in the tropics, had at that time

different requirements in regard to warmth, and were therefore able to live also in temperate latitudes; secondly, because, if our latitudes enjoyed a climate of tropical warmth in Tertiary times, the torrid zone must have had a hyper-tropical climate, which would have annihilated all life within it.

These objections cannot here be considered in detail, but the most important refutations of them may be brought forward.

(1) Modern biology has long since admitted that the chief factor determining the distribution of plants and of cold-blooded animals, and especially marine animals, is to be sought for in the conditions of temperature. Other conditions of life are, of course, of great influence, but they only accentuate the state of affairs primarily brought about by the temperature. Thus equality of temperature is, *cæteris paribus*, a distribution-bridge, inequality a distribution-barrier. The fauna of our tropical surface-water cannot spread from the tropics into temperate latitudes, and it is contrary to our most firmly established beliefs to assume that a fauna with a habit similar to that of the tropical fauna of to-day, and with, in the main, the same genera, can have lived in a temperate climate in Early Tertiary times. This may be especially illustrated by reference to the reef-corals, which form such a characteristic feature of the tropical fauna of to-day, precisely because of their invariable sensitiveness to less than tropical heat.

Great probability is lent to this view by the more and more pronounced separating-out of the Early Tertiary fauna into zonally disposed faunas, which took place during the Tertiary period. This point will be more fully discussed later on.

This view of the climate of the Tertiary period has been strongly corroborated by the researches of Murray and Irvine, according to which an abundant secretion of lime is only possible in a warm climate. That lime in solution is precipitated only to a slight extent in cold water, but in great abundance in warm water, is in itself only a chemical fact; but the circumstance that the animals of the higher latitudes secrete little lime, while tropical animals secrete it in abundance, at once gives the chemical fact a physiological significance. And, according to it, the formation of coral-reefs is possible only in water of tropical warmth.

We believe, therefore, that no change in the amount of warmth required by marine animals has taken place. The lovers of warm water, which were unable to endure the

cooling of the climate, died, or migrated towards the equator; while those that preferred cooler water, and had till then inhabited the subsurface-water, or, at all events, had not found their optimum of temperature in the surface-water, were now able to distribute themselves unrestrictedly over the whole surface and subsurface-water of their former habitat. There is no ground for the theory that the similarity of the faunas of higher latitudes depends on adaptation; the genera remained unchanged before and after the separation of the faunas, as is proved by the comparison of the successive faunas of Tertiary and recent times.

(2) We have now to consider the question whether science requires us to believe that, in the times when a climate of tropical heat prevailed in our latitudes, the equatorial regions must have possessed a hypertropical climate, which would make life impossible.

In the first place, we have no ground for assuming that the present-day temperature is the highest degree of warmth that tropical animals are capable of enduring, or even that it affords their optimum of warmth. On the contrary, we have observations enough to show that tropical animals can very well endure a temperature considerably higher than that of the tropical surface-water. We know, too, that along the continental west coasts the cold currents extend into the tropical zones, and that, within these, cold deep water wells up, and the warmth of the surface-water is thereby materially lessened. As the causes of these horizontal and vertical water-movements are not local but telluric, they have held good for all ages. We can therefore imagine that, at a time when the surface-water on the east coasts was actually uninhabitable by living beings on account of its great heat, there may have been, in the regions of the continental west coasts, a climate which animals with the same warmth-requirements as our present-day tropical animals could quite well endure.

It has also been shown that it is in no way proved, as many have assumed on *a priori* grounds, that the same difference of temperature must have existed between the temperate latitudes and the equinoctial zones in the Early Tertiary or the Later Cretaceous period as obtains at the present day. This question has been discussed by me from the climatological point of view and by Dubois from the cosmological. These discussions do not, however, lie within the scope of our present problem.

Other Views.

This is perhaps the fittest place to discuss some of the other views which have a bearing on the question before us. A few investigators have admitted that it is necessary to assume a climate of tropical warmth in our latitudes to explain the Early Tertiary fauna; some of these, however, regard it as a local phenomenon, while others call in the aid of cosmic changes on a large scale.

There is on the whole earth no other spot where all the factors which make for the amelioration of the climate and the warming of the surface-water are combined in anything like the same degree as on the Western and North-western coasts of Europe; it seems impossible to find conditions better fitted to bring about this result than those now prevailing; so that in general this objection is hardly entitled to serious consideration.

Other investigators incline to the view that the earth's axis has so altered its position either within the earth itself or in relation to the earth's orbit that the climatic zones of earlier geological times were quite differently arranged, and may have shifted periodically over the earth's surface. But astronomers refuse to admit the possibility of variation on such a scale, and geology and palæontology offer no evidence of it. Moreover, from the palæontological records of the Tertiary period it can be proved that there is no ground for such an assumption, at least in regard to that period, with which we are alone concerned.

We are now in a position to see that there is no argument of any weight against regarding the Early Tertiary fauna as one of tropical habit. We have further seen that a climatological consideration of the problem excludes the theory that the fauna was a local one. Geological-palæontological inquiry yields the same result, inasmuch as the Early Tertiary faunas of tropical habit have been demonstrated from the most different parts of the earth, even from the southern hemisphere. We have accordingly to assume that in those times a climate of tropical warmth, with a fauna of tropical character, extended over the greater portion of the temperate zones.

Origin of Zonally-disposed Faunas.

Now that we have seen that the climatological consideration of the Early Tertiary by reference to its faunistic materials is a scientifically justified standpoint, we have every ground for maintaining this standpoint with regard to the

faunistic variations of the Later Tertiary also. And if palæontology teaches us that towards the close of the Early Tertiary in our latitudes the components of the Early Tertiary fauna of tropical habit disappear, that in the Middle Tertiary in our latitudes a fauna is found which resembles the present Mediterranean fauna in habit, and that, finally, in the more recent Tertiary the character of the fauna approaches more and more closely to that of our present-day fauna, then we may, indeed we must, assume that corresponding climatic changes underlie these faunistic variations.

A gradual shrinking-back of the tropical climate from its former wider domain must have brought about a zonally-disposed separation of the Early Tertiary fauna, inasmuch as only those members of the old fauna as were able to endure the lowering of the temperature could remain behind. The zonal disposition of the marine benthos-fauna of the present day is quite distinctly marked over the whole earth, although the definiteness of this is influenced by the development of local faunas. Then we have every reason to argue retrospectively and to assume that all the zonally disposed faunas of the earth have had the same cause, and that they have all originated through a zonal separating-out of the Early Tertiary fauna.

This theory becomes a certainty when we consider circumboreality. There is a large number of species which occur both in the North Atlantic and the North Pacific Oceans, without, however, extending into the arctic or torrid zones; indeed, there are similar boreal-European, East American, West American, and North Japanese species on the one hand, and, on the other, similar South-European and Japanese species. Now it cannot be seriously maintained that in recent Tertiary or still later times there may have existed in the boreal or warmer temperate zone a connexion between the Atlantic and Pacific through America or Asia; but the theory that similar relics of the Early Tertiary fauna must have remained at places of similar climate at once explains every peculiarity in the palæontological data, and it is quite indifferent whether at the time of the separation of the faunas the different boreal regions of the Atlantic and Pacific side were wholly and impassably separated from each other or not. If we have thoroughly grasped the historical conception of the evolution of faunas, particular cases of notal circumpolarity, such as we find developed at the southern extremities of the continents, at once become intelligible.

Finally, we have to go a step further, and assume, on the authority of palæontological observations, that in the later

Cretaceous period the old fauna with the habits of our present-day tropical fauna extended further northwards than in Early Tertiary times. Our studies have already shown us that we cannot regard such a condition as a purely local one, and so we arrive at the theory that in the middle of the Cretaceous period a climate of tropical warmth must have prevailed over the whole region of the present temperate zones.

Surface- and Subsurface-Fauna in Tertiary Times.

Up to this point we have characterized the Early Tertiary fauna quite generally as one of tropical habit; this brief designation now requires further analysis. If we make a table of the genera of molluscs (the molluscs form, above all other classes, the material skeleton for all palæontological and zoo-geographical studies of marine fauna) from the Early Tertiary in our latitudes, and note their distribution in the present surface-water, we find among them genera which now occur only in the surface-water of the tropics; but beside these are components of subtropical habit, of the habit of our North Sea forms, and, finally, also boreal and even arctic genera which never occur in the surface-water of warmer regions. But the Early Tertiary fauna cannot be compared with the surface-water fauna of the tropics; it corresponds rather to the surface-water fauna plus the subsurface-water fauna. If, nevertheless, we still characterize it as a fauna of tropical habit, we are justified by the consideration that in the tropics, and nowhere else on earth, warm-water, cool-water, and cold-water animals may occur quite close together, may, indeed, be disposed vertically under one another.

It is a question whether the strict separation between the surface- and the subsurface-fauna obtaining in the tropical fauna of the present day already existed in the fauna of the Early Tertiary; there seems much to be said on both sides. We may, however, leave this question open until exact statistics regarding it are compiled, and this for two reasons. First, supposing that the subsurface-fauna of the Early Tertiary extended into the region of the surface-water and mixed with its fauna, the change of climate during the Tertiary period would have brought about exactly the same consequences so far as the present-day fauna is concerned, as if the separation of the faunas into surface- and subsurface-faunas had taken place before the change of climate. So far as our present study is concerned, it is quite indifferent whether the subsurface-water fauna was actually or only potentially in existence in the Early Tertiary period; in

either case the forms most capable of resisting cold, and therefore best suited to a cooler environment, would remain in their old habitat.

Secondly, although the separation of the surface- and subsurface-water faunas in the warmer regions of the earth appears to be fairly distinct, the Mediterranean forms an exception. Quite half the molluscs of the western shores of Norway and fully a quarter of those of the coasts of arctic Norway occur in the Mediterranean; but it is quite out of the question that in the Mediterranean they live only in the deeper layers of constant temperature. It is of course possible that faunistic displacements occur according to the season, so that Mediterranean animals of northern and arctic character live in the surface-water only in winter; on comparatively steep shores the distance, for many at least, would not be too long. Unfortunately I know of no data on this last point so far as it affects the benthos animals. Nevertheless the state of affairs in the Mediterranean confirms our conclusion that the separation between surface- and subsurface-*fauna*, whether it be actual or only potential, is not of supreme importance.

Circumtropicity of the Earlier Tertiary Fauna.

And now that nothing more stands in the way of the recognition of our Early Tertiary fauna as one of tropical habit, we come to the question of the development of its circumtropicity. The surface-water fauna of our tropics is circumtropical, and this holds true of by far the greater number of genera and even of many of the species. The similarity of many species from the Indo-Pacific and West-Indian seas, and, on the other hand, from the eastern and western shores of Central America, proves to us that the modern separating conditions have not sufficed to efface circumtropicity, and that, if these separations were suddenly to disappear, the circumtropicity would be expressed throughout the whole region to a much more perfect degree.

Thus the surface-water fauna of our present tropics is the remains of the Early Tertiary fauna shrunk back into the equatorial zone; it lives in approximately the same thermal conditions as the ancestral fauna enjoyed in our latitudes. On what possible grounds, then, can it be asserted that circumtropicity was less developed in the Early Tertiary fauna than in the present surface-water fauna of the tropics?

No one doubts that the subsurface-fauna of the Early Tertiary, whether it was actually or only potentially developed, may have been distributed over the whole area of

sufficiently cool water, since this quite agrees with the now prevailing conditions of the subsurface-water fauna.

We must accordingly expect to find in the oldest and earlier middle Tertiary a large number of species identically occurring in the northern and southern hemisphere—for instance, in our own region and in South Australia. If we simply compare the lists that have been drawn up, this certainly does not seem to be quite the case; but if we take account also of the remarks made by the authors, we find that there is a large number of species closely allied to and difficult to distinguish from those of the Antipodes of a similar age. When, further, we recall that the palæontologists of different countries have very often named their species with little or no reference to the work of their colleagues, we have to admit that the circumtropicity of the earlier Tertiary faunas was so strongly marked that it extended not only to the great majority of genera, but, in a great many cases (whose number future studies will probably increase), even to species. And thus it is certain that the Early Tertiary fauna had an approximately similar uniform expression or representation throughout the whole region of its distribution.

"Universal" Faunas.

The palæontologists of the newer school are for the most part strongly opposed to the theory of faunas of cosmopolitan or universal character. Of course, if by a fauna of universally or uniformly similar character any person means one which exhibits in every locality throughout its region a similar combination of genera and species, he is asking more from Nature than it is reasonable to expect, and neither zoologist nor palæontologist can agree with him. We have, however, on the earth at the present day two universal or uniformly differentiated surface-water faunas which we know thoroughly —the arctic and the tropical—and through these we can best learn to recognize the characters of a uniformly differentiated or "universal" fauna. In the arctic fauna circumpolarity is exhibited by a large percentage of species, and we get the impression that it has hitherto been prevented in a considerable percentage more by some hindrance or other, and that if all distribution-barriers were swept away circumpolarity, and therefore universality, would reach the highest possible degree of development within the arctic zone. Even in the arctic fauna, notwithstanding its pronounced circumpolarity, local differentiations have developed, and also local varieties and races; but it seems quite certain that, if the local causes

were removed, these would be extinguished, and would merge themselves into the general circumpolarity.

The case is the same with the tropical surface-water fauna; the faunas of the West Indies and of Panama were not always separate, as they are now, for in pre-Miocene times the West Indian overlapped that of Panama and has left its traces there to this day. Thus we see that the absolute circumpolarity of the tropical surface-water fauna is present but latent, and that it is exhibited as soon as a possibility of wider distribution arises. And if we consider aright the enormously wide distribution of the uniform tropical fauna from the east coast of Africa to the Pacific Islands, we see that, if the continent of Africa were to sink, or to be broken up into a tropical archipelago, the tropical fauna would spread itself over that region also. All that we learn from the tropical fauna goes to show that the local gradations, even those exhibited by West Africa and tropical West America, would disappear if the distribution-barriers were removed. And therein the "universality" of a fauna lies—not in the development of an absolutely similar combination at every spot in its region, but in the fact that the potentiality to this exists, and becomes a reality as soon as the hindering causes disappear. The development of local faunas in no way affects the existence of a contemporaneous and coextensive "universal" fauna.

Besides these two surface-water faunas there is a universally developed subsurface-water and deep-sea fauna, both of which we know less thoroughly than those already treated of. There is also a universally differentiated pelagic fauna of the warmer seas. The works of Keller and Brandt on the Suez Canal and the Baltic Canal show us the rapidity with which the spreading of a fauna takes place in similar climatic conditions after the removal of the barriers to distribution. Furthermore, the forward and backward displacements of the northern and arctic faunas during the Glacial periods are well known.

There are certainly palæontologists who do not agree to the limitation of the conception of a universal fauna which I have here proposed; but these must remember one thing—so long as they look on fossils as stones they may have an opinion with regard to their distribution founded only on their observations, but as soon as they begin to see in the fossils the living beings of an earlier epoch they must take the standpoint of modern biology—that is to say, they must work along with biologists and rely upon the well-established results of biological observation.

Further, the supporters of the theory of the permanency of climatic faunas must remember that it is plainly irreconcilable with the modern doctrine of evolution. If the individual climatic faunas had developed each for itself from the very beginning of the world, the types, wherever arising, could never have spread over the whole earth; each faunistic region would have had its own phylogenetic history from the oldest pre-Cambrian times till now. This, however, does not accord with any palæontological picture whatever, nor with that afforded by recent zoology and botany.

We have hitherto based the theory of the universal character of the Early Tertiary fauna on palæontological data, and on the relations of that fauna to the present tropical surface-water fauna. We now come to a third consideration.

Bipolarity.

Nearly all authors who have worked at the fauna of the higher southern latitudes speak of the great "habit-resemblance" of this fauna to that of the higher northern latitudes. This likeness is, however, impaired by the fact that the South-American and Australian faunas send their southern stragglers into these regions; further, the extraordinarily slight development of circumpolarity renders the presentment of a complete picture of the fauna as a zonally disposed whole extremely difficult; and, lastly, we know nothing of the fauna of the real antarctic.

In the year 1890 I attempted a sketch of the surface-water fauna of the higher southern latitudes compared with that of the higher northern latitudes, which, apart from the errors and inaccuracies involved in statistics of that nature, presents a fairly complete picture of the scientific data at that time, for it is based on the collected literature and on the works of authoritative writers.

This work brings out two points which are of essential importance in judging of the resemblances—first, the resemblances in the various divisions of the animal kingdom are very unequally expressed, being in some cases quite surprising and in others hardly noticeable; secondly, even the absence of many families and genera distributed over the warmer seas contributes to increase the habit-resemblance of the two faunas of the higher latitudes. For the theory we are now occupied with, that all the climatic faunas have arisen from a separating-out of the Early Tertiary or pre-Tertiary fauna—that is, through a kind of selection—a negative resemblance is quite as important as a positive one, though it is less evident.

In 1896 Sir John Murray published a very minute investigation into the distribution of all the species occurring in the Kerguelen region, and his results agree entirely with mine. On that occasion he also collected the remarks of various writers on this subject, and showed how strongly the likeness between the forms of the higher southern and higher northern latitudes has impressed many.

On the publication of the 'Ergebnisse der Magelhaensischen Sammelreise' the editors expressed their sense of the importance of this point by the request that every worker at a group should take account of its arctic-antarctic relations. Schaudinn and Römer expressed the same wish in the programme for the publication of the results of their Spitzbergen expedition.

The papers which appeared in the 'Ergebnisse der Magelhaensischen Sammelreise' and in the publication of the results of Plate, Nordenskiöld, and some others on the animals of higher southern latitudes have not altered in its essential features the picture which I sketched in 1890. The same holds true of other hitherto unpublished investigations, which have been communicated to me verbally, and, further, of my own work, which for some time has never been interrupted, on the rich material of the Hamburg Museum, which every year receives new and important contributions from the southern point of South America. One thing can be affirmed with decision—that the theory of the great similarity of the faunas of higher northern and southern latitudes receives new support from the working out of nearly all groups; and the accord between the two faunas extends to hundreds of genera.

Of the genera which occur as members both of the arctic-boreal and subantarctic-notal faunas, a number are found within the equatorial regions either in the surface- or subsurface-water, but a considerable number are absent from this region. Of the numerous species occurring *both* in the higher northern and southern latitudes, on the other hand, only a few are distributed through the tropics. In my paper of 1890 I have called those species and genera which are absent from the equinoctial zone, and which, owing to the discontinuity of their representation, especially demand explanation, "bipolar," and their mode of distribution "bipolarity."

Let us now return to a point which we reached earlier in our study—namely, that palæontological records show a great accord between the Early and Middle Tertiary of Central Europe on the one hand, and of South Australia and the great Australian islands on the other. This similarity extends, among Mollusca probably, among Bryozoa

certainly, in some cases even to species. If we find the Early Tertiary fauna, whose composition was "universal," developed as far as the latitude of Copenhagen in our hemisphere, there can hardly be any objection to the assumption that in the southern hemisphere it was developed to similar latitudes, and in that case it must have embraced all the localities which now make up the area of the so-called subantarctic fauna. When, owing to the gradual cooling of the climate in the course of the Tertiary period, the components of the old fauna of tropical habit withdrew from the higher latitudes, and those remaining in the old place formed a zonally-disposed relict-fauna, according to their power of resistance to low temperature, identical or similar forms of course remained behind in the corresponding northern and southern latitudes, and not similar genera only but similar species. Both from our own and from the Australian Mid-Tertiary we know a number of species which have persisted to the present day. In the same way quite a considerable number of species have remained unaltered on the east and west coasts of Central America since the Miocene period; and there is nothing to prevent our assuming that, in the higher northern and southern latitudes also, a number of species may have remained unaltered from the Mid-Tertiary till now, and this could take place as well in the north as in the south, so that, at the present day, identical species occur in the northern and southern latitudes.

If the components of the Early Tertiary faunas of tropical habit withdrew from our latitudes towards the end of the Early Tertiary, this process of selection or separating-out must have taken place in higher latitudes proportionately earlier, in the true polar zone certainly in the Cretaceous period, if not before it. Now, no one assumes that animal species (here I exclude the Protozoa) have remained unchanged from the earliest Cretaceous period, or farther back, until the present day. And if certain species actually occur in higher southern latitudes which are also known from the Arctic fauna, it is simplest to assume that these animals did not remain behind in the polar zone in Mesozoic times, but that they remained in the cooler temperate region in Tertiary times, and thence extended their distribution towards the pole.

It may here be mentioned that it is not necessary to picture the corresponding stages of the separation of the faunas as quite simultaneous in both hemispheres; the result is the same though corresponding phases in north and south may not have taken place at exactly the same geological time.

Deep-Sea Fauna.

Reasons of a theoretical kind, which I have elsewhere analyzed, make it probable that the peopling of the deep sea with living creatures first took place from the polar zone in Mesozoic times. Observation shows us that, even now, animals from higher latitudes—by no means all, but very many—descend to the deep sea. The peopling of the deep sea from the polar zone has thus been an uninterrupted process from the Mesozoic age till now. Therefore we find in the deep sea a mingling of either archaic or highly adapted—*i. e.* certainly very old—forms with those of the same habit as our present polar animals. Of an *Eryon*-like Crustacean or a *Salenia* I can say with certainty that it belongs to the old immigrants, and with probability I can say the same of those quite peculiarly adapted deep-sea fishes of the families of the Ophidiidæ, Macruridæ, Murænidæ, and so on. But I cannot affirm it of a *Leda* or *Neæra*, for these genera date from the Palæozoic or Mesozoic age and are still living; the species in question or their ancestors may belong to the oldest or most recent migrants to the deep sea.

If I find a species in the deep sea in the northern hemisphere which still lives in the surface-water of the arctic or boreal zone and there only, I can say that the immigration is of comparatively recent date; but if the species is already known from the Mid-Tertiary, I am forced to say—and with the greatest probability—that the immigration dates from the middle of the Tertiary period; for there is no reason why a species which descends to the deep sea to-day should not have so descended at any period of its existence. The probability that the deep-sea species of arctic origin did not migrate in the present-day period is increased by the fact that now, by suboceanic upheavals, the polar zone in the Pacific Ocean is absolutely, and in the Atlantic almost entirely, shut off from the deep sea of the temperate zone.

The age of the great majority of marine species dates back to the Tertiary, perhaps even to the Mid-Tertiary period. We may therefore assume, even in the case of species whose palæontological age we do not know, that the process of their migration into the deep sea occurred in Tertiary times, and that this process has certainly gone on in the south uninterruptedly to the present day, while in the north it has now become considerably restricted.

Now, for *Mid*-Tertiary times the similarity of species in our latitudes and in South Australia is established by palæontological research. If we find one of these species in the deep sea

we cannot say whether it has migrated from the north or from the south; but as every migration demands time, we can assume with some probability that those occurring in the temperate zone of the northern hemisphere have come from the north, and those in the southern from the south. But if it were the case that the time which a species requires to migrate over the whole deep sea from one polar zone to the other were trifling in comparison with the length of its sojourn in the deep sea, one could no longer say that an example found near Scotland came from the north, and one found near South Georgia came from the south. But this is not at all how matters stand. Murray has compiled exact statistics of distribution for the Kerguelen region; I myself have extended these for the whole earth, though they are still far from being complete. But one thing seems fairly well established, that practically all the unipolar surface and subsurface animals of the higher north and south, which descended into the deep sea, have penetrated to the borders of the tropics or into the tropical zone, but not beyond it into the opposite hemisphere. An example known to most zoologists is furnished by the genus *Serolis*, of which many species are developed in the notal surface-water, and a still greater number in the deep sea, yet its range, apparently, does not extend beyond the equator.

It would seem, therefore, that the time which has elapsed since the present surface-water species of the higher north and south descended to the depths has not sufficed for a migration beyond the equator to the opposite hemisphere; the exceptions to this rule disappear almost wholly, if not wholly, on closer consideration, although for certain species of Sponges, Worms, and Bryozoa we must assume an age extending beyond the middle Tertiary period—and this is in no way at variance with the facts.

Subsurface-Fauna.

We have now to deal in a few words with the subsurface, in the same way as we have dealt with the deeper water. We know that in Early Tertiary times a universally homogeneous fauna extended over the tropics and the temperate zones. Thus the similar species of north and south had a continuous connexion through the tropical zone. This continuity through the tropical zone was probably kept up in part through the deep water. As within the tropical zone at the present day, the fauna of northern habit is found exclusively in the subsurface-water (we shall have to consider later the peculiar conditions of Western America), nothing is more obvious than that there

exists even now a continuous connexion through the subsurface-water of the tropics between the identical genera and species of the higher latitudes. Curiously enough, this is corroborated by actual observations only in part as regards genera, and not at all as regards species. And so it seems certain, just as in the case of the deep sea, that the species occurring alike in the surface-water of the higher northern and southern latitudes have in general in the tropics an interrupted discontinuous distribution, notwithstanding the fact that it must have been continuous up to *Mid*-Tertiary times.

The remarkably poor development of the fauna of the tropical subsurface-water, as revealed by deep-sea investigations, gives us a hint as to the cause of this phenomenon. The reason of this retrogression may lie in the extraordinary development in the tropics of reef-facies, which, absorbing almost all the supplies of the surface-water, may have overwhelmed the other members of the old fauna, or crowded them into the deeper water: the forms adapted to the region of light perished, the mud-eaters went down to the deep sea. Thus the subsurface-water fauna by no means corresponds to the surface-fauna of higher latitudes, but only to the mud-eating portion of it. The change in the internal economic conditions of this community, the gradually enforced economic dependence on an altered surface-water fauna, and the change of the mud-bottom to one of coral-mud, must assuredly have worked towards the impoverishment of the fauna; but a still stronger influence must have been exerted by the probable scantiness of nutrition in the coral-mud, which had already passed through the food-canal of fishes as pieces of lime, and of echinoderms as coral-sand.

Now the coral-reefs are not developed on the west coasts of Africa and America, so that we might expect to find there the continuity in distribution of at least some bipolar species, which is rendered difficult, if not altogether suppressed, within the coral-region. But the state of the subsurface-water fauna of Africa is practically unknown; though Von Maltzan mentions the stunted growth of the Senegambian forms of *Pleurotoma* as compared with the same species from the Mediterranean *. We have gained some knowledge of tropical West

* Professor Chun, in his admirable work on the German Deep-sea Expedition ('Aus den Tiefen des Weltmeers,' Jena, 1900, p. 75), says concerning the nature of the West-African coast:—"We were less satisfied with the results of the trawling operations, which we made to depths of 4900 m. The bottom of the deep sea in these regions is covered with a disagreeable, viscous, blackish ooze, apparently mixed with the mud

America through the researches of the 'Albatross,' but there still remains too much to be worked up to allow us to suggest reasons why a subsurface-water connexion between the similar forms of north and south has not been discovered on the western shores of tropical America. Possibly such a connexion may some day be established for one or other group of animals. If, personally, I doubt this, it is for two reasons. In the Panama province there is certainly no coral-reef formation, but there is a surface-water fauna of tropical character, and in times not very long gone by there was really coral-formation. The reasons for a more or less marked suppression of the subsurface-water fauna by the tropical surface-fauna may hold good in this case also to a greater or less degree.

Secondly, corresponding to the remarkably equable climate, we find, on the west coast of America from the temperate southern to the temperate northern zone, a fauna of nearly homogeneous character, interrupted only in the narrow province of Panama. In general character it may be described as a cool-water fauna, but it has undergone quite remarkable local differentiation. This fauna springs, apparently, from the southern hemisphere; and thus, probably in ancient days, possibly before the time of the separation of the faunas, this fauna of southern origin gradually conquered its present region—that is to say, it crowded out more or less the members of the universal fauna.

Thirdly, Agassiz expressly mentions the poverty of the depths examined by him on the 'Albatross.' He accounts for this by the fact that the currents on the tropical shores of West America waft in a comparatively limited quantity of pelagic organisms, which would afford food for the inhabitants of the deep sea. As the animal world of the deep sea is wholly, and that on the slopes of the continents partly, dependent economically on the pelagic fauna, we have here a reason of great importance, and one which would apply in the main to West Africa also. In the same way, it must be taken into account that the extreme narrowness of the continental slope affords anywhere the opportunity for an interruption of faunal continuity.

I cannot omit to refer here to a fact which may be brought

carried out by the great African rivers." Probably the bottom of the continental slope shows these river-deposits in a still higher degree, so that we may have a similar state of affairs as, for instance, on the east coast of temperate South America, where the mouths of the Rio Negro and Rio La Plata form barriers between the South Brazilian and the Patagonian littoral and continental faunas.

forward in connexion with the discontinuity of the cool-water fauna in the subsurface-water of the tropics—namely, the influx of subterranean rivers. As most subsurface animals may dispense with pelagic larval stages, submarine river-mouths would possibly form barriers to distribution. And in general I wish to call attention to the fact that all the conditions which may have contributed to the impoverishment of the tropical subsurface-fauna need not extend over the whole area to bring about this result.

Pelagic Fauna.

Finally, I should like to touch, in a few words, on the bipolarity of the pelagic animals, although this does not really form part of our present theme. The theory has been promulgated, on the strength of isolated results, that the bipolar plankton species only seem to be bipolar, but really have a continuous distribution either through the deeper water (Chun) or in the surface-water (Lohmann) of the tropics. No objection can be offered to either assumption in itself; the Early Tertiary condition would have persisted till the present day, just as has occurred exceptionally among benthos forms. Moreover, all the objections which have been cited above against a general meeting of northern and southern forms in the subsurface-water of the tropics refer to conditions which affect the benthos animals alone. But it is certain that a connexion through the deeper water is scarcely possible for the plankton plants and the animals directly dependent on these. Therefore this theory yields no general principle of explanation applicable to the whole of the conditions. But we know enough to be justified in assuming that there was in Early Tertiary times a pelagic fauna of almost universal distribution and composition, and that, therefore, the presence of similar genera and species of plankton animals and plants in the higher latitudes of the earth must date back to the Tertiary period. The pelagic fauna of higher latitudes may therefore be looked upon as a relic of the Early Tertiary fauna, and the connexions now existing through the tropics offer no explanation of the existing plankton conditions of higher latitudes, but are to be regarded either as likewise relics of the Early Tertiary fauna or as local and relatively transitory pushings forward of the fauna of higher latitudes.

Objections to the Theory of Bipolarity.

The position we have reached is thus as follows:—There

is in the tropical zone a considerable discontinuity in the distribution-region of several hundre ls of genera of surface-water animals occurring in the higher northern and southern latitudes, and also in the distribution of very many—in any case far more than a hundred—species of higher latitudes. Either the discontinuity is really present in the tropical zone, or it appears to be so because of the present incomplete state of our knowledge. The reasons for the first supposition we have already discussed. Reasons in favour of the second case undoubtedly exist also, and I believe that, with the further progress of our knowledge, some regions of distribution which are now believed to be discontinuous will be found to be continuous. But that this may prove so in all cases is an assumption which receives no justification either from general considerations of probability or from the present state of our knowledge. And it is not only our right, but our duty to base our theoretical assumptions on the state of knowledge at the time. But even if we go the length of assuming that all bipolar genera and species may disappear from science, will that affect a single point in our theories of the relation of the arctic and antarctic faunas? The Early Tertiary roots of our present fauna remain the same whether bipolarity exists or not; and the similarity between the faunas of higher latitudes also remains the same, whether the distribution-regions of the genera or species be continuous or not.

The possibility, however, that a continuous distribution through the deeper waters of the tropics may be demonstrated for all the coeval surface-water inhabitants of the higher northern and southern latitudes is simply not to be thought of. The marine plant-world of the higher latitudes exhibits quite a pronounced bipolarity; and the idea that this should extend through the lightless layers of the tropical subsurface-water beyond the equator cannot be entertained. The same, of course, holds true of all animals which are directly dependent on the plant-world. So that, as a general principle of explanation, we may dismiss the hypothesis that the surface-water animals of higher latitudes have a continuous distribution through the deeper layers of the subsurface-water of the tropics. This, of course, does not prevent us from supposing that the assumed connexion, which must have existed at one time, does actually occur in some cases at the present day, both in the deeper strata and in the surface-water.

There is still another possible way in which the examples of bipolar genera and species, which have hitherto been present in literature, may disappear from science; that is, by

the breaking-up of the genera and species in question into two or more. But what precise extension is given to the terms genera and species is purely a matter of taste; the actual facts are in no way affected. Further, whether we have to do with actual or assumed continuity in time and space, the warrant for the conception of species disappears: for historical-geographical considerations it is too contradictory; the ideas of species as something separating, and of development in time and space, are incommensurable. Thirdly, for the purpose of our present study it does not matter at all whether the representatives are regarded as identical species, or as different forms of the same species, or as nearly related species. The point is in the evidence of close relationship, and it does not matter much what systematic expression we give to this fact.

Conclusion.

We have now reached the end of our study. We have seen that the faunas of higher latitudes represent the coeval relics of the almost uniformly developed and almost universally distributed Early Tertiary faunas, as they have been evolved under the influence of the cooling of the climate, by a process of separating out and selection. The similarity of the operating causes secured that the same components of the old fauna remained behind in both north and south; and thus has arisen the great and still well-marked similarity of the two faunas.

XLI.—*On a Collection of Spiders from the Bahama Islands made by J. L. Bonhote, Esq.; with Characters of a new Genus and Species of* Mygalomorphæ. By F. O. Pickard Cambridge, B.A.

[Plate VII.]

A small but valuable collection of Arachnida was made in the neighbourhood of Nassau by Mr. Bonhote and presented to the British Museum. Amongst other interesting forms were two adult males of the family Theraphosidæ, large hairy spiders locally termed Tarantulas. For these a new genus has been made, and the species is also new: it is characterized by the presence of stridulating-spines on the trochanters of the first pair of legs and the palpus.